Tree height and hydraulic traits shape growth responses across droughts in a temperate broadleaf forest

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Table 1. Summary of hypotheses, corresponding specific predictions, and results. We count predictions as fully supported / rejected when the response matches/contradicts the prediction in both univariate and all top multivariate models (when applicable). Parentheses indicate that predictions were partially supported/ rejected–i.e., that the direction of response matched/contradicted the prediction but that the effect was not significant in all models.

	Prediction supported?				
Hypotheses & Specific Predictions	Overall	1966	1977	1999	Results
H1.0. Larger-diameter trees have lower drought resistance (R).					
1.0 - R decreases with stem diameter.	yes	yes	(yes)	(no)	Table 4
H1.1. Tall trees have lower drought resistance.					
1.1 - R decreases with height (H).	yes	yes	(yes)	(no)/(yes)	Tables 4, 5
H1.2. Trees with more exposed crowns have lower drought resistance.					
1.2a - Dominant trees have lowest R.	(yes)	yes	(yes)	(no)	Tables 4, 5
1.2b - Correcting for H, dominant trees have lowest R.	(no)	(no)	(yes)	(no)	Tables 4, 5
H1.3. Small trees (lower root volume) suffer more in drier microhabitats.					
1.3 - There is a negative interactive effect between height and TWI.	(no)	(no)	(no)	(no)	Table 4
H2.1. Species traits predict drought resistance.					
2.1a - Wood density correlates negatively to R.	(yes)	(yes)	(yes)	(no)	Table 4
2.1b - Leaf mass per area correlates positively to R.	(yes)	(yes)	(no)	(yes)	Table 4
2.1c - Diffuse porous species have lower R than ring-porous.	(yes)	(yes)	(no)	yes	Tables 4, 5
2.1d - Percent loss leaf area upon desiccation (PLA) correlates negatively with R.	yes	yes	(yes)	(yes)	Tables 4, 5
2.1e - Turgor loss point correlates negatively with R.	(yes)	(yes)/(no)	(yes)/yes	(yes)	Tables 4, 5
H2.2. At the community level, taller trees have more drought-resistant traits.					
2.2a - Community mean wood density correlates negatively to H.	yes	-	-	-	Table S5
2.2b - Community mean leaf mass per area correlates positively to H.	yes	-	-	-	Table S5
2.2c - Community fraction of diffuse porous species decreases with H.	no	-	-	-	Table S5
2.2d - Community mean PLA correlates negatively to H.	no	-	-	-	Fig. 2e, Table S5
2.2e - Community mean turgor loss point correlates negatively to H.	no	-	-	-	Fig. 2f, Table S5
H2.3. When traits are accounted for, taller trees still have lower drought resistance.					
2.3 - R decreases with H when traits are included in the statistical model.	yes	yes	(yes)	(yes)	Table 5
H3.1. Resistance differs across the droughts considered here.					
3.1 - Drought year explains variation in R.	no	-	-	-	Fig. 1b, Table 4
H3.2. The direction of responses to predictor variables differs across droughts.					
3.2 - Directions of responses to best predictor variables differ across droughts.	rarely	-	-	-	Tables 4,5
H3.3. The strength of responses to predictor variables vary across droughts.					
3.3 - Best predictor variables differ across droughts.	yes	-	-	-	Table 5

Table 2x. Summary of variables

variable	symbol	units	description	category	n	observed values: median	min	max	ln-transformed?
Dependent variable									
drought resistance	R	-	ratio of growth during drought year to mean growth of the 5 years prior.	-	1596	0.87	0	1.99	no
Independent variables									
drought year	Y	-	year of drought	1966	478	-	-	-	-
				1977	547	-	-	-	-
				1999	571	-	-	-	-
tree size									
diameter breast height	DBH	cm	DBH in drought year	-	all	31.92	3.92	134.19	yes
height	H	m	H in drought year	-	all	20.21	4.76	43.87	yes
microhabitat									
crown position	CP	-	2018 crown position	dominant (D)	31	-	-	-	-
				co-dominant (C)	231	-	-	-	-
				intermediate (I)	224	-	-	-	-
				suppressed (S)	101	-	-	-	-
topographic wetness index	TWI	-	steady-state wetness index based on slope and upstream contributing area	-	all	5.66	0	16	yes
species' traits									
wood density	WD	g cm-3	dry mass of a unit volume of fresh wood	-	all	0.62	0.4	1.09	no
leaf mass per area	LMA	kg m-2	ratio of leaf dry mass to fresh leaf area	-	all	48.69	30.68	75.8	no
xylem porosity	XP	-	vessel arrangement in xylem	ring	408	-			-
				semi-ring	31	-			-
				diffuse	178	-			-
turgor loss point	TLP	MPa	water potential at which leaves wilt	-	all	-2.39	-2.76	-1.92	no
percent loss area	PLA	%	percent loss of leaf area upon dessication	-	all	13.06	8.52	24.64	no

Table 3. Overview of analyzed species, their productivity in the plot, numbers and sizes sampled, and traits. Given are DBH mean and range of cored trees, the number of cores represented by each crown position of each species, and mean hydraulic trait measurements.

species	percent.ANPP	n.cores	mean.DBH_cm	DBH.range_cm	xylem.porosity	PLA_percent	LMA_g.per.cm2	TLP_Mpa	WD_g.per.cm3
Liriodendron tulipifera	47.1	109	36.9	90.4	diffuse	19.56	46.92	-1.92	0.40
Quercus alba	10.7	66	47.2	67.7	ring	8.52	75.80	-2.58	0.61
Quercus rubra	10.1	71	54.9	136.9	ring	11.01	71.13	-2.64	0.62
Quercus velutina	7.8	83	54.1	98.2	ring	13.42	48.69	-2.39	0.65
Quercus montana	4.8	67	42.2	76.7	ring	11.75	71.77	-2.36	0.61
Fraxinus americana	3.8	69	35.4	88.3	ring	13.06	43.28	-2.10	0.56
Carya glabra	3.7	39	31.4	88.7	ring	21.09	42.76	-2.13	0.62
Juglans nigra	2.1	31	48.1	62.8	semi-ring	24.64	72.13	-2.76	1.09
Carya cordiformis	2.0	17	27.2	50.8	ring	17.22	45.86	-2.13	0.83
Carya tomentosa	2.0	18	21.0	20.1	ring	16.56	45.36	-2.20	0.83
Fagus grandifolia	1.5	81	23.5	96.0	diffuse	9.45	30.68	-2.57	0.62
Carya ovalis	1.1	24	35.3	51.1	ring	14.80	47.60	-2.48	0.96

Table 4. Univariate models

variable	category	null variables	all droughts		1966		1977		1999	
			dAICc	coefficients	dAICc	coefficients	dAICc	coefficients	dAICc	coefficients
drought year	1966		-2.42	0.0000	-	-	-	-	-	-
	1977		-	-0.0209	-	-	-	-	-	-
	1999		-	-0.0105	-	-	-	-	-	-
ln[DBH]		Y	8.17	-0.0385	15.32	-0.0888	-0.87	-0.0214	-1.93	0.0057
ln[height]		Y	8.17	-0.0620	15.32	-0.143	-0.87	-0.0345	-1.93	0.0092
crown position	D	Y	-2.96	-0.0461	3.25	-0.0509	0.66	-0.0759	0.38	-0.0103
(alone)	C		-	0.0000	-	0	-	0	-	0
	I		-	-0.0063	-	0.0732	-	-0.0298	-	-0.0563
	S		-	0.0122	-	0.0526	-	0.0432	-	-0.0483
crown position	D	ln[H]+Y	0.57	-0.0347	-1.84	-0.0328	-0.23	-0.073	3.04	-0.0024
(with height)	C		-	0.0000	-	0	-	0	-	0
	I		-	-0.0425	-	0.0139	-	-0.0388	-	-0.081
	S		-	-0.0582	-	-0.0662	-	0.0258	-	-0.0956
ln[TWI]		ln[H]+Y	5.34	-0.0890	-1.96	-0.0171	5.05	-0.1404	2.8	-0.1033
ln[TWI]*ln[H]		ln[H]+ln[TWI]+Y	-0.83	0.0824	-1.58	0.0958	-1.47	0.089	-1.9	0.0428
wood density		ln[H]+Y	-1.91	-0.0479	-1.24	-0.2089	-1.22	-0.1812	0.22	0.2502
leaf mass per area		ln[H]+Y	-1.99	0.0003	-1.88	0.0012	-1.76	-0.0013	-2	0.0004
xylem porosity	ring	ln[H]+Y	-2.68	0.0583	0.81	0.1542	0.42	-0.1874	3.97	0.1998
	semi-ring		-	-0.0244	-	-0.1112	-	-0.1386	-	0.1493
	diffuse		-	0.0000	-	0	-	0	-	0
turgor loss point		ln[H]+Y	1.33	-0.1777	-1.64	-0.1078	1.26	-0.25	0.016	-0.1732
percent loss area		ln[H]+Y	7.17	-0.0140	9.18	-0.0249	-0.05	-0.0105	-0.716	-0.0074

Table 5. Summary of R$\hat{2}$ and coefficients of the best multivariate models for each drought instance. Models are ranked by AIC, and we show all models whose AIC value falls within 2.0 of the best model (dAICc<2).

					crown position					xylem architecture				
drought	dAICc	R2	Intercept	ln[H]	D	C	I	S	ln[TWI]	diffuse	semi-ring	ring	PLA	TLP
all	0.000	0.12	1.085	-0.059	-	-	-	-	-0.086	-	-	-	-0.012	-0.113
	0.371	0.12	1.401	-0.061	-	-	-	-	-0.087	0	0.164	0.049	-0.018	-
	0.586	0.11	1.373	-0.057	-	-	-	-	-0.086	-	-	-	-0.013	-
	0.726	0.12	1.232	-0.092	-0.034	0	-0.037	-0.051	-0.079	-	-	-	-0.012	-0.101
	0.813	0.11	1.493	-0.092	-0.034	0	-0.039	-0.054	-0.079	-	-	-	-0.014	-
	1.051	0.13	1.508	-0.095	-0.032	0	-0.038	-0.052	-0.08	0	0.149	0.051	-0.017	-
1996	0.000	0.27	2.401	-0.151	-	-	-	-	-	0	0.428	0.159	-0.039	0.284
	0.837	0.27	1.564	-0.151	-	-	-	-	-	0	0.142	0.137	-0.025	-
	1.443	0.25	1.641	-0.14	-	-	-	-	-	-	-	-	-0.025	-
	1.599	0.27	2.546	-0.176	-0.034	0	0.012	-0.069	-	0	0.442	0.162	-0.039	0.31
	1.972	0.27	2.439	-0.151	-	-	-	-	-0.017	0	0.434	0.16	-0.039	0.288
1977	0.000	0.22	0.346	-	-0.074	0	-0.027	0.042	-0.131	0	-0.331	-0.23	-	-0.384
	0.090	0.21	0.393	-	-	-	-	-	-0.14	0	-0.324	-0.234	-	-0.369
	1.506	0.22	0.449	-0.023	-	-	-	-	-0.137	0	-0.314	-0.226	-	-0.37
1999	0.000	0.24	1.042	-	-	-	-	-	-0.1	0	0.261	0.191	-0.01	-
	0.123	0.25	1.280	-0.072	0.004	0	-0.076	-0.091	-0.088	0	0.242	0.195	-0.009	-
	0.370	0.24	0.533	-	-	-	-	-	-0.098	0	0.077	0.181	-	-0.161
	0.913	0.24	1.143	-0.071	0.002	0	-0.077	-0.092	-0.09	0	0.146	0.202	-	-
	1.142	0.22	0.902	-	-	-	-	-	-0.102	0	0.161	0.199	-	-
	1.485	0.24	1.153	-0.08	0	0	-0.081	-0.096	-	0	0.235	0.196	-0.01	-
	1.586	0.26	1.063	-	-0.005	0	-0.05	-0.041	-0.097	0	0.232	0.183	-0.009	-
	1.714	0.24	0.645	-0.079	-0.001	0	-0.081	-0.095	-	0	0.054	0.186	-	-0.162
	1.821	0.26	0.580	-	-0.006	0	-0.051	-0.041	-0.095	0	0.059	0.174	-	-0.154
	1.878	0.25	0.827	-	-	-	-	-	-0.099	0	0.187	0.186	-0.006	-0.073

References

Helcoski, R., Tepley, A. J., Pederson, N., McGarvey, J. C., Meakem, V., Herrmann, V., Thompson, J. R., and Anderson-Teixeira, K. J. (2019). Growing season moisture drives interannual variation in woody productivity of a temperate deciduous forest. *New Phytologist*, 0(0).

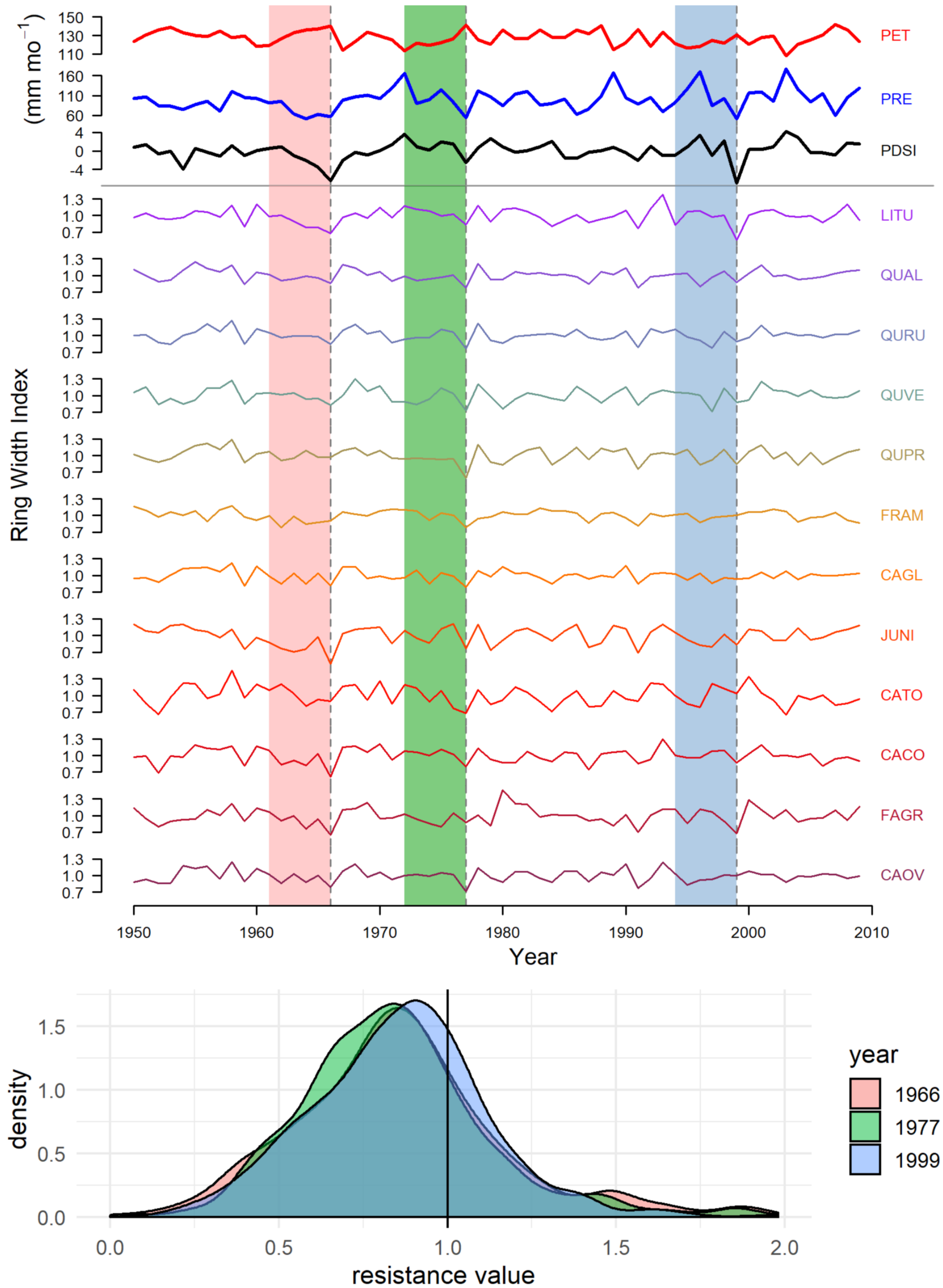

Figure 1. Climate and species-level growth responses over our study period, highlighting the three focal drougths (a) and community-wide responses Time series plot (a) shows peak growing season (May-August) climate conditions and residual chronologies for each species. Focal droughts are indicated by dashed lines, and shading indicates the pre-drought period used in calculations of the resistance metric. Figure modified from (Helcoski et al., 2019). Density plots (b) show community- wide resistance values for each drought.

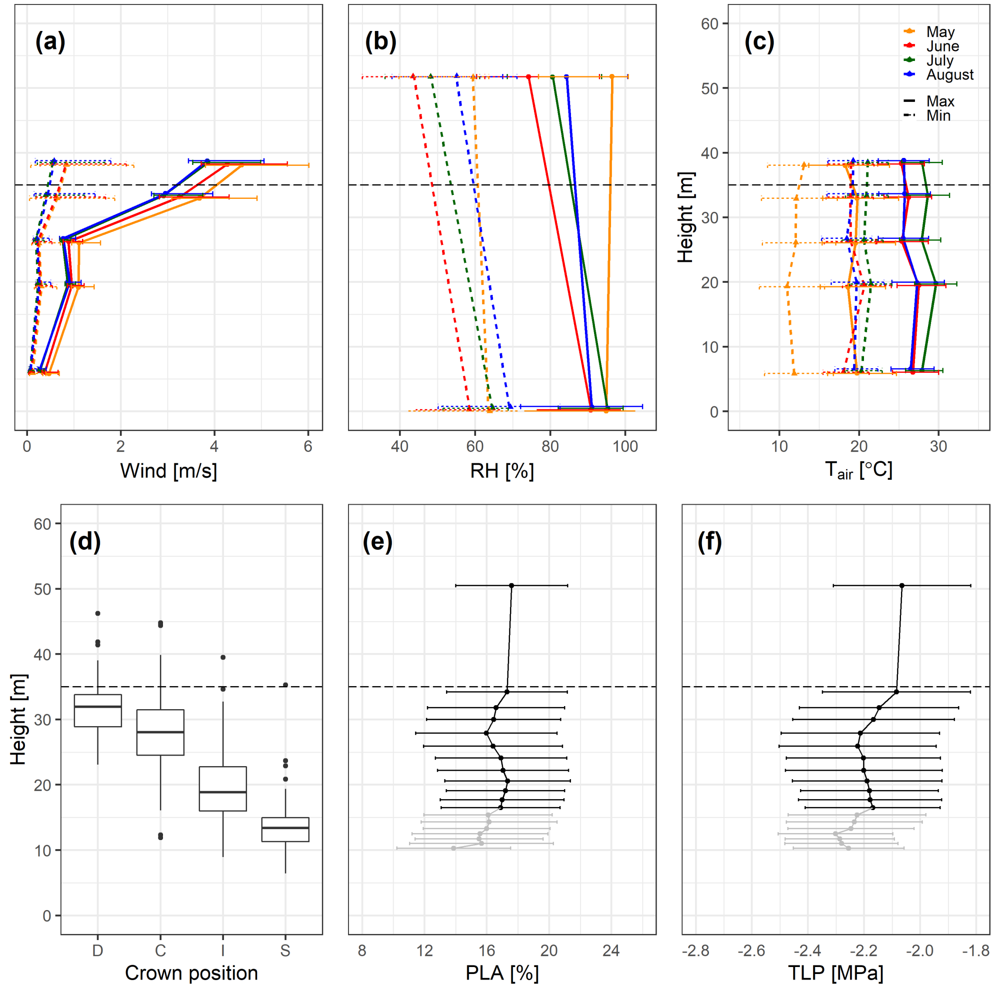

Figure 2. Height profiles in growing season climatic conditions, tree heights by crown position, and leaf hydraulic traits The top row shows averages (± SD) of daily maxima and minima of (a) wind speed, (b) relative humidity (RH), and (c) air temperature (T_{air}) averaged over each month of the peak growing season (May-August) from 2016-2018. In these plots, heights are slightly offset for visualization purposes. Also shown are (d) 2018 tree heights by canopy position (see Table 2 for codes) and vertical profiles in (e) PLA_{dry} and (f) π_{tlp}. In (e-f), values are community-wide averages across height bins (plotted at upper end of height bin), with grey indicating bins for which species-level trait measurements are available for <75% of individuals. In all plots, the dashed horizontal line indicates the 95th percentile of tree heigts in the ForestGEO plot.